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Alloparental care in social muroid rodents

Vladimir S. Gromov

ABSTRACT. The article concerns fitness effects of alloparental care, or helping (i.e., assistance of young individuals in rearing offspring that are not their own) in social muroid rodents (*Meriones unguiculatus*, *Microtus ochrogaster, Microtus pinetorum*, *Lasiopodomys mandarinus*, *Peromyscus polionotus*, and *Rhabdomys pumilio*) that are characterized by a family-group lifestyle and biparental care. According to inclusive fitness theory, alloparenting may alter both direct and indirect fitness. In particular, helpers may benefit indirectly if breeders that receive assistance subsequently produce more offspring. In laboratory studies, however, neither the presence of alloparents nor greater numbers of alloparents affected litter size at weaning. The results of the experimental studies also provide little support to the hypothesis that breeders benefit directly by increasing their lifetime reproductive success. In some species, helpers may decrease the workload of breeders, but the effects of alloparenting were found to be slight and often mixed. However, there is evidence that alloparental care yields direct benefits to helpers by providing experience that allow them to become more successful parents. It seems unlikely that helping behavior evolved merely to kin selection in consistence with 'Hamilton's rule'. A more appropriate explanation is that helping behavior in rodents is a by-product of the evolution of sociality, i.e. the transition to a family-group lifestyle with biparental care. Extended family groups with helpers form due to delayed dispersal of offspring, and the latter may gain direct and/or indirect fitness benefits from staying within their natal groups. Alloparenting could be considered a form of cooperation due to which both breeding pairs and their older offspring being helpers may gain direct or indirect fitness benefits.

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Помощничество у социальных мышевидных грызунов

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РЕЗЮМЕ. В статье рассматривается влияние помощников (молодых особей, помогающих взрослым ухаживать за детенышами из младших выводков) на приспособленность у социальных мышевидных грызунов (*Meriones unguiculatus, Microtus ochrogaster, Microtus pinetorum, Lasiopodomys mandarinus, Peromyscus polionotus* и *Rhabdomys pumilio*), для которых характерны семейно-групповой образ жизни и забота о потомстве у самцов и самок. Согласно теории совокупной приспособленности, помощничество оказывает влияние как на прямую, так и косвенную приспособленность. В частности, помощники могут получать косвенную выгоду, если размножающаяся пара произведет больше потомства. Однако в лабораторных условиях ни наличие помощников, ни их число не влияли на размер приплода. У некоторых видов помощники способствуют снижению физической нагрузки на особей-производителей, однако этот эффект слабо влияет на приспособленность. Результаты проведенных экспериментальных исследований слабо подтверждают гипотезу о том, что размножающиеся особи получают прямую выгоду за счет увеличения репродуктивного успеха. Однако забота о чужих детенышах может быть полезной для помощников благодаря приобретенному опыту ухаживания за потомством. Поведение помощничества у грызунов, по-видимому, является побочным продуктом эволюции социальности, т.е. перехода к семейно-групповому образу жизни, а не результатом родственного отбора в соответствии с известным «правилом Гамильтона». Сложные семейные группы с помощниками формируются благодаря задержке расселения молодых особей, которые получают прямые или косвенные преимущества, оставаясь в составе семейных групп. Помощничество следует рассматривать как одну из форм кооперации, благодаря которой и размножающиеся пары, и их потомство из старших выводков, выступающее в качестве помощников, получают прямые или косвенные преимущества, повышающие их индивидуальную приспособленность.

КЛЮЧЕВЫЕ СЛОВА: грызуны, родственный отбор, помощничество, преимущества и издержки.

Introduction

In cooperatively breeding mammals, young individuals assist in rearing offspring that are not their own through activities such as feeding, carrying, babysitting, and pup thermoregulation (Emlen, 1991; Solomon & French, 1997). Such a behavior is called alloparenting, or helping. The presence of alloparents within social groups, common among many communally rearing and monogamous species (Kleiman, 1977; Emlen, 1982, 1991; Brown, 1987), is a phenomenon that deserves study, since the reproductive costs born by nonbreeding individuals are theoretically at odds with an individual reproductive strategy. This apparent anomaly does not contradict the theory of inclusive fitness (Hamilton, 1964), in which an individual's overall or inclusive fitness is the sum of both direct benefits to the individual in propagating their own offspring (direct component) and indirect benefits by helping to propagate the offspring of related kin (indirect component; Brown, 1987). Hamilton (1964) showed that natural selection of genes will lead to individuals behaving in a way that maximizes their inclusive fitness rather than their own or direct reproductive success. Maynard-Smith (1964) coined the term 'kin selection' to describe the process by which characteristics are favored due to their effects on relatives.

In behavioral ecology, alloparenting is considered a reproductive altruism which is costly to the actor and beneficial to the recipient (Davies *et al.*, 2012). If the actor suffer cost C and the recipient gains a benefit B as a result of the altruistic act, then the gene causing the actor to behave altruistically will increase in frequency if $r \times B - C > 0$, where r is the coefficient of relatedness of the actor to the recipient. This result is known as 'Hamilton's rule' (Charnov, 1977). Put into words, altruistic cooperation can be favored if the benefits to the recipient (B), weighted by the genetic relatedness of the recipient to the actor (r), outweigh the costs to the actor (C).

If an individual has a choice between rearing its own offspring and helping its mother to produce offspring, the expression above becomes $B/C > 1$, assuming that the individual's own offspring and its mother's offspring, both have $r = 0.5$. Therefore, helping will be favored by kin selection if by the individual's help its mother produces more extra offspring than the individual has 'sacrificed' through providing help. It is necessary to emphasize that kin selection isn't just about genetic relatedness (r); it is also about the ecological factors that determine the cost (C) and benefit (B) of behaviors (Davies *et al.*, 2012).

Several possible explanations that are not mutually exclusive may account for the evolution of alloparental care in singular cooperative breeders (i.e., groups in which only one female is breeding). The individual fitness hypothesis states that helpers benefit directly by caring for young but breeders and young do not benefit (Ligon, 1981; Woolfenden, 1981). According to the inclusive fitness hypothesis, helpers benefit indirectly by increasing the fitness of non-descendent kin (Brown, 1974; Emlen, 1978). Helpers may be contributing to their indirect fitness when they care for siblings, who are more likely to survive with the presence of helpers (Hamilton, 1964; Emlen & Wrege, 1989; Emlen *et al.*, 1991). Because they decrease the workload of breeders, helpers may benefit indirectly if breeders that receive assistance have higher survivorship (Rood, 1990; Bales *et al.*, 2000), subsequently produce more litters or have shorter inter-litter intervals (Solomon, 1991; Powell & Friend, 1992; Bales *et al*., 2001; Russell *et al*., 2003). It is also hypothesized that alloparental care yields direct benefits to helpers by providing experience that will allow them to become more successful parents (Lancaster, 1971; Snowdon & Cronin, 2007). This hypothesis predicts that alloparenting experience results in an increased quality or quantity of future offspring as well increased reproductive success due to acquisition of parental skills. Another adaptive hypothesis for alloparental care predicts that breeders benefit directly by increasing their lifetime reproductive success (Brown, 1987). Helpers may benefit indirectly if their behavior increases the reproductive output of younger siblings. This benefit may be realized, for instance, through increased survivorship of younger siblings. Incurring direct benefits does not preclude indirect benefits and vice versa. It has been also hypothesized that helping behavior is an unselected by-product of the evolution of parental care (Jamieson & Craig, 1987; Jamieson, 1991).

Several studies have sought evidence supporting the hypothesis of inclusive fitness as an adequate explanation for the presence of helpers remaining as non-reproductive members in extended family groups (Koenig & Pitelka, 1981; Emlen, 1991; Brown, 1987). A few correlational studies have also provided evidence for the enhancement of the kin or indirect component of inclusive fitness by demonstrating of positive correlation between the number of helpers and the number of younger siblings surviving to maturity in a variety of avian and mammalian species, except for rodents (Salo & French, 1989). In particular, a study on gray-crowned babblers, *Pomatostomus temporalis* (Vigors & Horsfield, 1827), with an experimental manipulation involving the direct removal of helpers has shown that intact groups with helpers successfully raised more young, than those with helpers removed (Brown *et al.*, 1982).

Unfortunately, most of works regarding evaluation of direct and indirect fitness benefits of alloparenting has been conducted on avian and some mammalian species (mainly, primates and carnivores), while few studies have been carried out on rodents. As a result, there is a dearth of knowledge about benefits and costs associated with alloparenting to the helpers and breeders in rodents. This review is focused on fitness effects of alloparenting and its evaluation in terms of benefits and costs in several social muroid rodents, including *Meriones unguiculatus*, *Microtus ochrogaster, Microtus pinetorum, Lasiopodomys mandarinus*, *Peromyscus polionotus,* and *Rhabdomys pumilio*. The results of these studies are also considered in the context of

conceptual models that explain the evolution of alloparental care in rodents.

Overview of helping behavior in muroid rodents

Helping behaviors monitored for juveniles in different studies on rodents usually include (1) brooding pups (crouch over pups, cover them with ventral body surface), (2) grooming pups (manipulate pups with forepaws while licking pups' body surfaces), (3) retrieving pups (grasp pup with incisors along the back of the neck, carry or drag pup back to nest), (4) caching food (carry or drag food to establish or maintain a stockpile), (5) maintaining the nest (carry or drag materials into the nest, chew these materials into small pieces, push the pieces into the nest with the head and forepaws), and (6) maintaining runways (establish new runways by digging and kicking away the substrate, clean accumulated dirt and debris from existing runways). The results of studies that allow us to evaluate direct and indirect fitness effects of alloparenting in the aforementioned rodent species are presented below.

The Mongolian gerbil, *Meriones unguiculatus* (Milne-Edwards, 1867)

Mongolian gerbils live in extended family groups, and their social organization is characterized by persistent pair bonds, biparental care of the young and delayed offspring dispersal. Family groups usually include one adult male, one or two, less frequently three adult females, and their offspring. The total number of members in a large family group can amount to 28 individuals (Gromov, 2022). The number of young individuals in a group depends on the number of reproducing females who in spring and summer bring in as many as three litters, each including 4 to 7 young animals. The presence of the breeding pair is the main factor resulting in delay of sexual maturation and suppression of reproduction among the young individuals until dispersal. Young born in the spring disperse by the fall, but young born in the summer and early autumn remain in their family groups until the next spring (Ågren *et al.*, 1989; Gromov, 2022). The Mongolian gerbil is a cooperative breeding species: the male and female form an integrated parental unit when rearing their offspring (Elwood & Broom, 1978; Clark *et al.*, 1997; Gromov, 2009). Young gerbils that remain in the natal area become non-breeding helpers within the family group assisting in the rearing of the infants (Ostermeyer & Elwood, 1984; French, 1994). Specifically, young gerbils interact extensively with their younger siblings, exhibiting care-giving activities such as nest attendance, retrieving, huddling over and grooming pups. The presence of the helpers is thought to be beneficial to physical and behavioral development of the pups, and their major contribution appears to be warmth and additional tactile stimulation of the infants (Elwood, 1975; Gromov, 2009, 2020). It might be predicted, in particular, that the extra warmth in the nest provided by helpers would be beneficial, and that this should lead to faster development of the infants.

Ostermeyer & Elwood (1984) conducted an experimental study to examine the effects of the presence of young gerbils (helpers) upon the physical development of the younger siblings. The multiparous pairs housed together with a male and female juvenile from their directly preceding litters (i.e., family groups with helpers) were used as subjects of the study. On the day that a second litter in each breeding pair was born it was reduced in size to four pups. The number of pups surviving in each litter, as well as their body mass were recorded and compared with the relevant data obtained from multiparous pairs rearing their single litter of four pups (i.e., family groups without helpers). The study revealed no positive effects of the presence of helpers on survival and development of the pups. Moreover, infants suffered a retarded growth in the presence of helpers.

Salo & French (1989) carried out a study to examine a hypothesis that young gerbils that remained in their natal family group, and gained experience with younger siblings, would be more successful in raising their own litters than were individuals that did not have such experience. Experienced litters were allowed to gain exposure to a subsequent litter born to the breeding pair. The non-experienced young gerbils remained in the parents' cage but did not gain exposure to younger siblings. The results of the study indicated that early experience with younger siblings influenced reproductive performance, pup development, and parental behavior. The effects of early experience with younger siblings were more influential for male gerbils. Measures of pup body mass gain and eye opening both indicated that males that received early experience with younger siblings were better sires, as reflected in advanced pup development. Thus, the presence of an experienced male was directly beneficial for pup development. Besides, both the latency to reproduce the first litter, and the proportion of pairs giving birth within 50 days, suggest that individuals receiving experience with younger siblings enjoy a reproductive advantage compared to those pairs not receiving such experience. The results of this study support the hypothesis that extended residence by non-breeding helpers in family groups of the Mongolian gerbil contributes to the eventual individual, direct reproductive success of these individuals. These benefits for individual reproductive effort may overweight any potential contribution to the indirect component of inclusive fitness.

French (1994) conducted an experimental study to compare the reproductive and developmental consequences of the presence versus absence of helpers during the reproductive lifetime of breeding pairs. At the birth of the first litter, breeding pairs were assigned randomly to one of two treatment conditions: helpers present (HP) and helpers absent (HA). The weanling gerbils served as alloparental helpers. Data collection continued for 13.5 months after pairing, at which point breeders were 16.5–17 months old. Over the 13.5 months of the study, breeding pairs produced an average nine

litters, with mean litter size of 5.7 pups at birth. No significant differences between HP and HA groups were noted for any reproductive parameter. The results of this study show that the presence of helpers has little overall impact on the lifetime reproductive performance of breeding females or on rates of pup development. Pairs with helpers throughout their breeding lifetime had litter sizes, rates of pup production, mean and cumulative litter weights, and rates of pup injury and mortality that were similar to pairs without helpers. The author of this study concluded that the data obtained argue against a central role for indirect fitness in accounting for alloparental care and cooperative breeding in the Mongolian gerbil. Under the conditions in this experiment, few indirect benefits accrue to helpers as a consequence of their alloparental effort, and immediate (the opportunity for independent reproductive attempts) and delayed (parental skills acquisition) direct benefits may account for helping behavior in this species.

The prairie vole, *Microtus ochrogaster* (Wagner, 1842)

Prairie voles are a socially monogamous and biparental species that lives in family groups and maintain varied and often complex social structures (Gruder-Adams & Getz, 1985; Getz & Hofmann, 1986; Carter & Getz, 1993; Getz & Carter, 1996). For most of the year, approximately one-third of family units are single mothers, one-third are male/ female breeding pairs, and one-third are extended family groups (often called communal) consisting of a breeding pair and several reproductively inactive alloparents, usually elder offspring (Getz & Carter, 1996). Partner preference behavior is well characteristic of prairie voles, but pair bonding is not the only type of family-relevant behavior displayed by these rodents. Nest sharing, mate guarding, paternal and biparental care, spontaneous alloparenting, and communal nesting are also exhibited (Getz *et al*., 1981, 1993; Getz & Carter, 1996; Roberts *et al.*, 1998; Lonstein & De Vries, 1999). Juveniles are highly philopatric: 68 % of the males and 75% of the females remain at their natal nest (Getz *et al.,* 1987). Typically, one to three juveniles remain at the nest while parents produce a subsequent litter (Getz *et al.,* 1987). At least at low population density, female, and possibly also male, juveniles are reproductively suppressed and do not breed (Carter & Getz, 1985). As for alloparental care, juveniles spend a significant amount of time in the natal nest, so that the litter is seldom left alone. Juveniles also show active forms of parental behavior such as retrieving, huddling over and grooming younger pups. Besides, juveniles contribute to nest and run way construction (Thomas & Birney, 1979; Gruder-Adams & Getz, 1985; Getz *et al.*, 1987; Solomon, 1991).

Solomon (1991) conducted an experimental study that was designed to investigate potential indirect fitness benefits that may accrue to juvenile prairie voles as a result of alloparental care of younger siblings. Breeding pairs were randomly assigned to treatment (juveniles present or absent). Juveniles consisted of pups from a pair's first litter. All juveniles were removed in the 'juveniles absent' treatment, whereas two randomly selected juveniles (one of each sex if possible) were allowed to remain in the 'juveniles present' treatment. The age at which a pup's eyes were fully opened was used as an index of developmental rate. The inter-litter interval and subsequent litter size were also recorded. It was found that pups gained more weight and their eyes opened sooner when juveniles were present. Pups reared with juveniles were about 13% heavier at weaning than those reared without juveniles. In family groups with juveniles, pups were alone in the nest less often than in groups without juveniles. Besides, presence of juveniles was associated with reduced inter-litter intervals if females had reared a large litter previously. The results of this study demonstrate potentially important mechanisms that may produce indirect fitness benefits to juvenile prairie voles as a result of their participation at the natal nest. Both infants and parents benefited from the presence of juveniles, suggesting that helping may enhance the helper's indirect fitness in multiple ways.

Stone *et al*. (2010) carried out an experimental study to test the hypothesis that alloparental experience as juveniles enhances later parental care and reproductive success in the prairie vole. The authors of this study examined whether voles that had experience as juveniles caring for younger siblings would be more successful as parents than inexperienced voles when they first became reproductive, and if this effect displayed a dose-response. They allowed juveniles to care for one litter of siblings, two litters of siblings or none. Specifically, it has been predicted that (1) voles that spent more time exposed to and caring for younger siblings would show greater levels of parental behavior than less experienced juveniles; (2) voles that had more exposure to younger siblings would experience greater reproductive success (e.g., larger surviving litters and heavier offspring). In this study, groups of focal juveniles undergoing different amounts of experience with younger siblings were assigned as follows. The 'zero exposure' subjects (0EX) were housed together with their parents until removed from their parents' cage at 20 days of age. Juveniles in the 'one exposure' (1EX) group were not removed from their parents' cage at 20 days of age, but allowed to remain with their parents and provide alloparental care to one subsequent litter of younger siblings until time of weaning. Juveniles in the 'two exposure' (2EX) groups were ear-tagged and culled to four, but allowed to remain with parents and care for two consecutive litters of younger siblings. Behavioral observations indicated that 1EX individuals were more alloparental than 2EX individuals, displaying more contact with pups. This suggests that alloparental behaviors do not increase in a linear fashion with experience, and that exposure to one litter of siblings may constitute sufficient alloparenting experience in this species of voles. Presence or absence of alloparenting experience as juveniles had some effects on later parental behaviors. Females in the 0EX treatment, paired with

0EX males, spent the most time in the nest. 1EX males (but not females) spent more time licking and grooming their pups. Litter size, litter biomass at birth and days to first litter were not affected by alloparenting experience. Pups with 1EX parents gained more body mass later in development than did other pups, suggesting that there may be subtler benefits to alloparenting experience. Similarly, pups with 2EX fathers gained more body mass earlier in development. Pups with 1EX and 2EX parents also tended to open their eyes sooner. These findings show that juvenile prairie voles appear to accrue some benefits via alloparenting experience. This effect, however, is not necessarily linear and exposure to one litter of siblings may be sufficient to affect later parental competence and reproductive success.

The pine vole, *Microtus pinetorum* (Le Conte, 1830).

Pine voles live in extended family groups (Fitzgerald & Madison, 1983). Field and laboratory studies have documented life-history characteristics common to cooperatively breeding species: stable population densities (Horsfall *et al.*, 1973), high survival rates (Hayne, 1977), low recruitment rates (Fitzgerald & Madison, 1983), slow maturation rates and small litter sizes (Lepri & Vandenbergh, 1986; Schadler & Butterstein, 1979; Fitzgerald & Madison, 1983), well-developed biparental care (McGuire & Novak, 1984; Oliveras & Novak, 1986), and delayed dispersal so that juveniles remain in family groups while subsequent litters are raised (Fitzgerald & Madison, 1983).

Powell & Fried (1992) carried out an experimental study and quantified how the presence of juvenile pine voles affected the growth and development of their younger siblings. Sexually inexperienced voles were paired, and the numbers of juveniles remaining with parents as potential helpers were manipulated after the first litter of each pair reached weaning age. The juveniles were left with parents until the subsequent litters were 21 days old. Then juveniles were removed, and the number of the subsequent 21-day-old litter was manipulated to provide another treatment. Treatments with zero, one, and two juveniles were as balanced as possible for litter sizes of juveniles before reduction. This study showed that pup body mass and growth rates were not affected by presence of juveniles, number of juveniles, or litter size. Number of juveniles present did not affect pup survival as well. There was no significant difference in inter-litter interval between the treatments. Treatment did not affect subsequent litter size, and litter size did not affect behavior of parents or juveniles in any treatment. However, pups without older siblings present were alone more than pups with older siblings during all observation periods. Neither treatment nor pup age affected time that individual juveniles spent with pups. Treatment had no overall effect on duration or frequency of brooding or grooming per juvenile.

This study showed that the levels of helping behaviors exhibited were not strongly affected by the numbers of juveniles (i.e., helpers). Juvenile presence did not increase pup growth or survival but did decrease inter-litter interval in the three-juvenile treatment. Significant benefits to pups may have appeared from juveniles brooding and grooming them while mothers were away from the nest. The authors of this study concluded that juvenile pine voles exhibited helping behaviors, but fitness effects of that help remained an open question. The data obtained provide little support for indirect fitness benefits being the selective force behind the evolution of cooperative breeding in pine voles. It is hypothesized that maturing pine voles usually gains the greatest probability of high lifetime reproductive success by remaining in its natal family group and burrow system (i.e., due to philopatry), accruing whatever benefits may be associated with delayed dispersal, and competing for vacancies in its natal or an adjacent burrow system. The limited availability of vacant tunnel systems and the high cost of digging new tunnel systems constrain dispersal in pine voles and have led to the evolution of cooperative breeding. The results of this study are consistent with a concept of cooperative breeding having evolved via individual selection for delayed dispersal.

The mandarin vole, *Lasiopodomys* (= *Microtus*) *mandarinus* (Milne-Edwards, 1871)

Mandarin voles are a socially monogamous species (Smorkatcheva, 1999; Tai *et al.*, 2001; Tai & Wang, 2001). During the breeding season, each burrow system is occupied by a family group consisting of one adult male, one to five adult females and their offspring (usually 1–3 juveniles per litter). Young typically remain at their natal territory at least up to 45–50 days and some of them even up to 70 days (Smorkatcheva, 1999). Reproduction within family groups is commonly restricted to one female and one male, with family-group founders exhibiting persistent pair bonds. Males engage in all care-giving activities observed in the female, except for nursing. Alloparental care, when juveniles assist the breeders in rearing younger siblings, is also typical of mandarin voles, and elder young demonstrate all direct (brooding, grooming, and retrieving) and indirect (digging and providing nest material and food) care-giving activities (Smorkatcheva, 2002; Smorkatcheva & Smolnyakova, 2004; Jia *et al.*, 2009; Song *et al.*, 2010).

Smorkatcheva & Smolnyakova (2004) conducted a study to evaluate the contributions of helpers to different activities (nest residence, digging, bringing objects into the burrow, and eating) in family groups of *L. mandarinus*. The family groups consisting of a pair plus young (up to 11 individuals) were under observation for 2–4 months. The observations revealed that both adult and young males were the primary baby-sitters exhibiting brooding and grooming pups. Among young voles, significant sex differences in their activities were found: young females spent more time in the nest and engaged in digging more frequently than young males. Besides, young females contributed to food and nest material transport more than other members of the family groups. Among both parents and offspring, females

ate more than did males. The results of this study show that the relative investment of offspring to different activities is primarily dependent on their sex. The data obtained provide evidence that young females perform some excess workload to be used up, potentially, by the breeding female. Unlike young females, young males were revealed to play rather passive role in burrow constructing and transport of objects, and their participation in alloparental care was primarily restricted to brooding and grooming pups. The authors of this study suggest that *L. mandarinus*' helping behavior in the form of digging and bringing nest material evolved due to benefits of delayed reciprocity or group augmentation, like in some other avian and mammalian species (Ligon & Ligon, 1978; Woolfenden & Fitzpatric, 1978; Brotherton *et al.*, 2001). This hypothesis predicts that individuals that would most likely to associate with young in the future should help most. In consistence with this hypothesis, the available field data provide evidence for the natal dispersion of male mandarin voles, whereas some young females may breed staying at natal territory (Smorkatcheva, 1999). As for helping behavior in the form of brooding and grooming pups, the authors of the study find it difficult to explain how this behavior is evolved (Smorkatcheva & Smolnyakova, 2004). Cooperative breeding in the mandarin vole seems to evolve via individual selection for delayed dispersal, as it was argued particularly for the pine vole, *Microtus pinetorum* (Powell & Fried, 1992). According to Smorkatcheva & Smolnyakova (2004), it seems to be unlikely that alloparental behavior in rodents may be a means of gaining parental skills that are of great importance for pup survival.

To test this suggestion, Wu *et al.* (2013) carried out a study to examine whether the alloparenting experience make *L. mandarinus*' helpers more successful parents than inexperienced individuals, and whether receiving alloparental care from older siblings positively affects the parental behavior at adulthood. This study showed that alloparental experience only enhanced maternal behavior such as nest building and huddling, and did not significantly affect levels of paternal care. This could be explained by that the male helpers were exposed to younger siblings at around 21 days which is possibly too young for them to express parental behaviors. One of the main results of this study is that different levels and phenotypes of alloparental care at different ages may contribute to parental behaviors at adulthood, which possibly resulted in the sex-specific effects of alloparenting experience. Another finding is that second litters receiving alloparental care from the first litter demonstrate lower levels of anxiety at adulthood. Besides, receiving alloparental care from older siblings enhances parental behavior at adulthood including huddling and pup retrieval. Individuals living together with and receiving alloparental care from older siblings exhibited higher levels of parental care in later life. This result may be because of increased total investment and social contact not only from the parents, but also from alloparents from the previous litter. In general, the authors of this study have confirmed that alloparenting during the prepubertal period increased levels of locomotor activity, sociability and maternal behavior in adult mandarin voles. Receiving alloparental care from older siblings decreased levels of anxiety, and promoted the expression of social and parental behaviors. Thus, alloparental care may play an important positive role in the development of anxiety-like, social and parental behavior of the mandarin vole. Siblings from the first and second litters benefit from each other because of the alloparental care provided by the first litter. Alloparenting increases inclusive fitness both to providers and receivers of alloparental care.

The oldfield mouse, *Peromyscus polionotus* (Wagner, 1843).

Oldfield mice are a monogamous rodent species that displays biparental care (Foltz, 1981; Margulis, 1997, 1998). Field studies provide evidence that breeding pairs remain together and rear multiple litters; males engaging in parental care exhibit such care-giving activities as nest building and huddling with pups (Foltz, 1981). Only limited details on age of dispersal and maturity are available for *P. polionotus*. According to Foltz (1981), multiple litters are present in nests. In some cases, a female might be pregnant, lactating, and have older offspring present simultaneously. Given these life-history parameters, and the finding of presumed consecutive litters in nests in the wild, it is likely that pups often remain with their parents beyond the age of sexual maturity and during at least part of the rearing of a litter of siblings. Furthermore, it is unlikely that a breeding pair will produce more than two or three litters in their lifetime. For a species with such limited breeding potential, actions that increase the survival probability of litters, particularly first litters, are likely to be advantageous (Margulis *et al.*, 2005). Maternal behavior was found to have a much greater effect on litter survival than paternal behavior does (Margulis, 1998). For *P. polionotus*, possible reasons for delayed dispersal and reproduction may include a shortage of suitable nest sites, increasing inclusive fitness via kin selection, and gaining experience by helping to rear sibling offspring (Margulis *et al.*, 2005).

Margulis *et al.* (2005) carried out an experimental study to examine the effect of exposure to sibling neonates during the subadult period on subsequent parental behavior and reproductive success in *P. polionotus*. To generate subjects for the experienced and inexperienced experimental groups, when the pups reached 20 days of age, the father was removed, but instead of removing all pups at this time, at least two pups (a female and a sibling of either sex) were left with their mother through the birth and weaning of the next litter. These individuals were removed from their mother at the weaning of the subsequent litter. Animals were then housed in same-sex groups until the start of the experiment. These females became the 'experienced' females. Those pups that were not left with their mother were removed at 20 days of age, and housed

in same-sex groups until eventual pairing. These females became the 'inexperienced' females, indicating that they had no prior exposure to younger pups before producing their first litter. Both experienced and inexperienced females were paired with non-inbred, inexperienced males. The results of this study showed that there was no significant difference in litter size at birth for experienced and inexperienced females. However, among the experimental pairings, the probability of litter survival was substantially greater for experienced pairs than inexperienced pairs. Experienced females spent significantly more time nest building than did inexperienced females. No significant differences for males or females in the amount of time spent in contact with pups, locomoting, or carrying pups based on experience were found. These findings suggest that young females who remain with their mothers through the rearing of a sibling litter gain direct fitness benefits through their increased chances of successfully rearing their own pups. The results of this study also suggest that it was experience with pups prior to reproduction that influenced litter survival. A female who remains with her parents through the rearing of a litter of siblings may be delaying her own reproduction, but gains the benefits of having experienced one litter, without the energetic and physiological costs she would have incurred had her first litter experience been with her own pups. Males paired with experienced females showed behavioral changes similar to those observed in their mates. Thus, for a short-lived rodent species, like *P. polionotus,* with a limited number of opportunities to breed, increased survival of offspring in the first few litters may substantially affect lifetime reproductive success.

The African striped mouse, *Rhabdomys pumilio* (Sparrman, 1784).

Striped mice are a small diurnal rodent with a widespread, although discontinuous, distribution across southern Africa (Skinner & Chimimba, 2005). Striped mice are facultatively group-living, displaying social flexibility (i.e., males and females switch social organization and mating strategies; Schradin *et al*., 2012). When population density is low, females favor solitary nesting due to the costs associated with reproductive competition, and males adopt a roaming strategy, soliciting matings but showing no paternal care (Schradin, 2008). In contrast, when population density is high, striped mice form complex social units comprising 3–4 breeding females and a single dominant territorial breeding male that, through provision of paternal care, can significantly increase offspring development (Schradin & Pillay, 2004, 2005). In addition to maternal and paternal care (Schradin, 2008) breeding females exhibit helping behavior in the communal nest (Schubert *et al.*, 2009). Moreover, philopatric juveniles of both sexes remain in the nest for a number of months after weaning and provide alloparental care to their younger siblings (Schradin & Pillay, 2004). Philopatric helpers participate in territorial defense, nest building (Schradin & Pillay, 2004) and huddling (Schradin, 2005; Scantlebury *et al.*, 2006; Schradin *et al.*, 2006).

Rymer & Pillay (2014) conducted an experimental study to assess the level of alloparental care provided by juvenile and subadult philopatric females and investigate whether these different aged females influence the development of paternal care of their younger brothers. The authors of this study predicted that, compared with juvenile helpers, subadult helpers would provide higher levels of alloparental care (e.g., huddling), thereby alleviating maternal workload. Another prediction was that sons reared by the mother and juvenile daughter would show greater paternal care to their own offspring later.

The study involved two phases. In Phase I, parentally experienced breeding pairs were established. Each pair produced three litters, each representing a different treatment. First, males and females raised their first litter together. At weaning of the first litter, mothers were subjected to a second treatment (mother + young juvenile helper), in which a daughter from the first litter was randomly selected and remained with the mother. The father and all remaining offspring were removed. The mother and juvenile daughter then raised the next litter of young together. For the third treatment (mother + older subadult helper), the original male and female pairs were re-established. At 20 day after pairing, the male was removed. 60-days-old subadult daughter from the first litter, which had been housed separately from the mother was randomly selected and returned to the breeding cage. The mother and subadult helper raised the next litter. The parental and alloparental care behavior of the mother and helper (juvenile and sub-adult) for the next litter was measured and analyzed. In Phase II, one sexually matured male (son) from each litter was randomly selected and paired with an unrelated mate. The paternal care behavior of sons was measured in the same manner as for mothers and helpers.

This study revealed that mothers raising their young together with older daughters spent more time near their pups and groomed pups for longer periods than mothers raising young with a young daughter. In contrast, mothers spent more time huddling when they raised pups with a young helper than when raising pups with an older helper. When the mother was away from the nest, the care provided by older daughters accounted for 24% of the total parental care, whereas young daughters provided just 6% of care. Thus, mothers, philopatric helpers and offspring all benefited from the provision of alloparental care. Philopatric helpers themselves gained direct benefits from reduced energy expenditure for thermoregulation (huddling) and had increased opportunities for developing parental care. The levels of alloparental care provided by philopatric striped mice and concomitant alleviation of maternal care was age-dependent. Females that raised young with a juvenile daughter provided high levels of care, twice that of females that raised young with an older daughter. Sons raised by mothers and juvenile helpers displayed the expected exaggerated levels of care also observed when mothers raised litters on their own.

While these results show the direct value of subadult daughters, juvenile daughters could contribute indirectly (e.g. nest maintenance) to alleviating maternal workload. The development of paternal care indicates that mothers do distinguish between the care provided by different aged helpers. Overall, the type of alloparental care provided by female striped mice is expected to change over their lifetimes, resulting in increased inclusive fitness through caring for siblings and acquisition of parenting skills.

Pillay & Rymer (2015) conducted another study to examine whether alloparental care enhances factors of ecological importance by assessing the emotional response (challenge of open space), social competitive ability (competing with conspecifics for resources) and spatial learning and memory (locating food in the environment) of female alloparental striped mice. These authors also investigated whether direct exposure to young is required to elicit these changes or whether these can be acquired vicariously by being housed with, or in close proximity to, a mother raising offspring on her own. It was hypothesized that alloparents would show behavioral and cognitive enhancements similar to parents. Subjects used in this study were parentally experienced breeding pairs. The results of this study showed that: (1) alloparent females were less anxious; (2) experience of raising pups improved the rate of habituation in a novel environment; (3) the provision of maternal and alloparental care potentially enhances the resource holding potential (the likelihood of one individual winning a fight in dyadic encounters), suggesting that breeders and alloparents might have a competitive advantage for exploiting transient food resources, which directly affects female fitness; (4) alloparent and breeder females located a food reward faster when landmarks were available and made fewer errors during the probe trial compared to females with no experience with pups. Therefore, experience with pups improved both short (working) and longer-term memory in striped mice; the enhanced cognition of alloparents and breeders suggests that they might be able to acquire resources faster and more efficiently. In general, the authors of this study demonstrated that alloparents benefit both behaviorally and cognitively from providing care to the same extent as breeders. Contact with pups enhanced cognitive and behavioral performance of nulliparous alloparent females.

General discussion

Cooperative breeding systems in mammals can be differentiated according to the number of adults per group that simultaneously engage in reproductive activity. Species in which several adults of either sex are likely to breed are described as 'multiple' breeders; species in which only one individual of each sex is likely to breed at any given time are described as 'singular' breeders. No doubt, all the species considered in this review belong to 'singular' breeders with helpers recruited from their offspring, and this recruitment is rather passive.

Field studies provide evidence that extended family groups in social muroid rodents form due to delayed offspring dispersal and natal philopatry by both sexes (Fitzgerald & Madison, 1983; Getz & Hofmann, 1986; Solomon & French, 1997; Smorkatcheva, 1999; Solomon, 2003; Gromov, 2022). Young individuals delay dispersal and remain philopatric because they may gain direct or indirect fitness benefits staying within their natal groups (Stacey & Ligon, 1987, 1991; Kokko & Johnstone, 1999). In these groups, offspring remain after weaning and participate in care of subsequent litters born to their mothers. It has been hypothesized that the formation of extended family groups reflects a compromise between the cost of dispersal versus the cost of foregoing reproduction and staying within the natal group (Nunes, 2007). However, such a behavioral strategy couldn't be considered a reproductive altruism (Davies *et al.*, 2012), because juveniles participating in care of younger siblings successfully reproduce later after dispersal. Moreover, they, in turn, may benefit from the assistance of their own helpers.

It is also important to note that in any species of social muroid rodents, the number of potential offspring of several helpers in the sum is not less than the number of their mother's offspring, and this does not correspond to the conditions under which 'Hamilton's rule' applies. The evolution of alloparenting among social muroid rodents is much more than intriguing because in some species exhibiting social monogamy (e.g., *Meriones unguiculatus, Microtus ochrogaster*) estrus females can visit adjacent home rages to mate with neighboring males or strangers. As a result, multiple paternity has been found in many litters (Solomon *et al*., 2004; Gromov, 2022). Therefore, the offspring from one litter may be related to succeeding litters only as half-siblings. Benefits that helpers might accrue by assisting parents in the rearing of younger siblings would, therefore, proportionately reduced. Thus, it is very difficult, if possible at all, to calculate the ratio of benefits and costs of alloparenting in social muroid rodents in terms of 'Hamilton's rule'.

According to the inclusive fitness theory (Hamilton, 1964), alloparenting or helping to care for younger siblings by older juveniles may alter both the indirect and direct fitness. In particular, helpers may benefit indirectly if breeders that receive assistance subsequently produce more offspring. In laboratory studies, however, neither the presence of alloparents nor greater numbers of alloparents affected litter size at weaning in Mongolian gerbils, prairie voles and pine voles (Ostermeyer & Elwood, 1984; Solomon, 1991; Powell & Fried, 1992; French, 1994; Hayes & Solomon, 2004). The only study on oldfield mice provides evidence that increased survival of offspring may substantially affect lifetime reproductive success (Margulis *et al.*, 2005).

Alloparents may benefit the breeders by increasing the quality of offspring produced. One measure of offspring quality is body size at weaning. Alloparental care may result in increased offspring size relative to offspring reared by a single female, as it was shown in

a study on prairie voles (Solomon, 1991). Large body size at weaning may result in numerous potential benefits. Offspring that are heavier at weaning survive better than offspring that are lighter at weaning (Solomon, 1991; Huber *et al.*, 2001). Offspring that are heavier at weaning also tend to be heavier as adults. These individuals are preferred as social, and presumably mating, partners (Solomon, 1993) and are likely to be able to out-compete male conspecifics for mates (Sheridan & Tamarin, 1988). Finally, weaning body mass of females affects the growth of the pups: females that were larger at weaning had pups that grew faster prior to weaning (Solomon, 1994). Increased size of weanlings was reported when prairie voles were raised with alloparents under environmentally challenging conditions (e.g., lower temperatures or limited food; Solomon, 1991; Hayes & Solomon, 2004), suggesting that cooperative breeding can increase the quality of the offspring produced by a female. However, this effect has not been found in other muroid rodents.

Presence of juveniles was found to be also associated with reduced inter-litter intervals in prairie and pine voles (Solomon, 1991; Powell & Fried, 1992). This finding suggest that alloparenting may enhance the reproductive success of breeders, but further studies need to be carried out for more strong support of this suggestion. Besides, juvenile prairie voles appear to accrue some benefits via alloparenting experience: males, in particular, spent more time licking and grooming their own pups. Moreover, pups with experienced parents tended to open their eyes sooner indicating enhanced reproductive success of the helpers (Stone *et al*., 2010). In the pine vole, benefits to pups may have appeared from juveniles brooding and grooming them while mothers were away from the nest (Powell & Fried, 1992). Thus, both infants and their parents appear to benefit from the presence of helpers in the family groups of prairie and pine voles, suggesting that alloparental care may enhance the fitness of both breeders and helpers.

As for Mongolian gerbils, presence of helpers has little overall impact on the lifetime reproductive performance of breeding females (French, 1994). However, early experience with younger siblings positively affected reproductive performance, pup development, and parental behavior of the helpers; these effects were more influential for male gerbils. These benefits for individual reproductive effort may overweight any potential contribution to the indirect component of inclusive fitness. Thus, alloparenting contributes to the individual direct reproductive success of the helpers (Salo & French, 1989). Delayed direct benefits (due to parental skills acquisition) may also account for helping behavior in Mongolian gerbils (Salo & French, 1989; French, 1994), oldfield mice (Margulis *et al.*, 2005), prairie voles (Stone *et al*., 2010), and male mandarin voles (Smorkatcheva & Smolnyakova, 2004).

In mandarin voles, alloparental experience only enhanced maternal behavior such as nest building and huddling, and did not significantly affect levels of paternal care. In this species, helping behavior has been suggested to evolve via individual selection for delayed dispersal (Smorkatcheva & Smolnyakova, 2004). However, other authors (Wu *et al.*, 2013) suggest that alloparenting increases inclusive fitness both to providers and receivers of alloparental care. In African striped mice, alloparenting results in increased inclusive fitness through caring for siblings and acquisition of parenting skills; alloparents seem to benefit both behaviorally and cognitively from providing care to the same extent as breeders (Rymer & Pillay, 2014; Pillay & Rymer, 2015).

In general, the results of the experimental studies on social muroid rodents provide little support to the hypothesis that breeders benefit directly by increasing their lifetime reproductive success: presence of helpers was associated with reduced inter-litter intervals in two species only – *M. ochrogaster* and *M. pinetorum* (Solomon, 1991; Powell & Fried, 1992). In same cases, helpers may decrease the workload of breeders, but the effects of alloparenting were found to be slight and often mixed. The results of some studies support the hypothesis that alloparental care yields direct benefits to helpers by providing experience that allow them to become more successful parents (French, 1994; Margulis *et al.*, 2005; Wu *et al.*, 2013; Rymer & Pillay, 2014; Pillay & Rymer, 2015). Alloparenting may also contribute to the individual direct reproductive success of the helpers (Salo & French, 1989; French, 1994; Margulis *et al.*, 2005; Stone *et al*., 2010; Rymer & Pillay, 2014; Pillay & Rymer, 2015). Thus, direct and indirect fitness effects of alloparental care appear to be species-specific or dependent on the experimental conditions.

To summarize, one can conclude that it seems unlikely that alloparental care in social muroid rodents evolved merely to kin selection in consistence with 'Hamilton's rule'. A more appropriate explanation is that the helping behavior is a by-product of the evolution of sociality (i.e., transition to a family-group lifestyle; Gromov, 2017, 2018). Extended family groups with helpers form due to delayed dispersal of offspring, and the latter gain direct or indirect fitness benefits staying within their natal groups (Stacey & Ligon, 1987, 1991; Kokko & Johnstone, 1999; Gromov, 2017, 2018). Alloparenting could be considered a form of cooperation due to which both breeding pairs and their older offspring being helpers may gain direct or indirect fitness benefits. The expression of both parental care and helping behavior might be governed by the same underlying genetic mechanisms (Linksvayer & Wade, 2005). Moreover, some forms of alloparenting in rodents like brooding and grooming pups were found to be stimulated by the physiological mechanisms related to epigenetic re-programming of behavior (Gromov, 2011, 2020). Future studies in this direction would be very useful for better understanding of the phenomenon under study, especially among 'multiple' breeders, like the Brandt's vole (Gromov, 2023). Besides, behavioral observations and experimental studies carried out on other rodent taxa, especially among caviomorphs, also would provide very valuable information to better un-

derstand the evolution of helping behavior in rodents, as well as many remaining questions regarding how alloparenting may affect individual fitness.

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